

THE EFFECT OF SIZE, TEMPERATURE, OXYGEN LEVEL AND
NUTRITIONAL CONDITION ON OXYGEN UPTAKE IN THE
SAND DOLLAR, *MELLITA QUINQUIESPERFORATA*
(LESKE)

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Because metabolism often represents a large source of expended energy, accurate measurement of metabolism is essential for construction of energy budgets. Metabolic processes, as measured indirectly by oxygen uptake, however, may vary with physical condition and physiological state. It is often difficult to assess the results of all these variables on metabolism, and some effects are either discounted or estimated.

Such estimations may be misleading, especially in echinoids, where relatively few studies have been made and where different species of echinoids may respond differently to certain variables. The purpose of this study is to obtain a relatively accurate estimation of metabolic energy expenditure in the sand dollar, *Mellita quinquesperforata*, by measuring oxygen consumption seasonally at ambient water temperatures, under various degrees of starvation, during the day and night, and at different oxygen concentrations on various size animals.

MATERIALS AND METHODS

For monthly measurement of oxygen consumption, five or six animals of various sizes were collected from Mullet Key, a sub-tidal, semi-protected sandy beach area along the Gulf of Mexico, adjacent to the mouth of Tampa Bay, Florida (27° 38' N; 82° 44' W). After allowing the guts to clear overnight, animals were placed in individual dishes containing either 200 ml (for small animals), 500 ml (for medium-sized animals) or 1000 ml (for large animals) of freshly aerated sea water. After 0.5 hr, a 1-cm layer of mineral oil (which blocks oxygen diffusion) was poured over the surface of the water. At this time, an initial water sample was taken from a dish with no animal (control). A known volume of water (approx. 30 ml) was removed from each dish at 1 and 2 hr after sealing; the water was gently stirred just before sampling. Oxygen in water samples was measured using the micro-Winkler method (Hoar and Hickman, 1967). Sea water used for all experiments was collected from the field and filtered through 0.22 μ Millipore filters before use. A constant temperature chamber (dimly lit) stimulated monthly environmental water temperatures and fluctuated less than 0.2° C during each experiment. Salinity varied little between experiments (33.0-34.9‰). After 2 hr, each animal was removed, weighed, and placed in a drying oven at 80° C. Dried animals were weighed and ground to powder in a Wylie mill. A small sample of this material was used for measurement of total nitrogen by the micro-Kjeldahl (Holland, 1964). Monthly rates of oxygen consumption are expressed on a wet, dry and total body nitrogen weight basis. Analysis of the

data was done on values obtained after 1 hour as tests showed *M. quinquesperforata* to be an oxygen conformer.

To ascertain how rate of oxygen consumption is affected by reduced oxygen tensions in sea water, animals of similar weight (7 g dry weight) were placed in dishes containing a known volume of sea water (100 ml) in ten experiments. The dishes were sealed with a lid through which an oxygen electrode was mounted. The rate of respiration in these closed dishes was measured every 10 minutes. The water was stirred during each reading by a magnetic stirbar located just beneath the oxygen electrode. The water temperature in all these experiments was 25° C.

In addition to monthly measurements using a closed system, the rate of oxygen consumption was measured in June in an "open" or "flow-through" system, similar to the one described in Hoar and Hickman (1967). Six animals were placed in individual dishes which were closed to general water circulation except for entrance and exit holes. Water entered the dishes and was continuously siphoned into stoppered Erlenmeyer flasks. The rate of flow through the dishes was measured each day and adjusted so that oxygen tension never fell below 80% saturation. Animals used in this experiment were acclimatized to summer water temperatures (29–33° C). Experiments were run at 15, 20, 25, 30, and 35° C. For each experimental temperature, the water in the flow-through apparatus was changed and different animals were used. Animals were not placed into the dishes until all feces had been expelled (usually overnight); oxygen readings were begun after animals had been held at experimental temperatures in the dishes for one day. Oxygen concentration was measured in the Erlenmeyer flasks using a Beckmann Field-Lab oxygen meter fitted with a platinum electrode. Readings were taken at 4-hr intervals for 48 continuous hours. The experimental temperature was maintained by placing the whole flow-through apparatus in a constant temperature chamber. A dim light switched on at 0700 hr and off at 2200 hr simulating day-night conditions. After each experiment, animals were removed from the dishes, weighed and dried as described above. Results from the flow-through system were compared with results from a closed respiratory system. One-hour closed system measurements were run at the same temperature at the beginning of each flow-through experiment.

The effect of starvation upon the rate of oxygen consumption was measured at different times of the year by starving animals in filtered sea water for periods up to 1 month. Water in the holding tanks was renewed every 2 days with freshly collected and filtered sea water. During starvation, water temperature in tanks simulated ambient temperatures. The oxygen consumption of animals which were starved for various times (5–30 days), was measured in a closed system.

Results of all oxygen uptake experiments are expressed as log-log linear regression equations with \log_{10} rate of oxygen uptake and \log_{10} body weight (wet, dry or body nitrogen weight) being the two variables. Slopes and intercepts from different seasons or experiments were compared using analysis of covariance (Snedecor and Cochran, 1971). Variances were checked with Bartlett's Chi-square (Snedecor and Cochran, 1971). For ease in comparing rates of oxygen consumption at different temperatures, pooled slopes were used when statistically valid and intercepts were adjusted as follows; new intercept equals average of Y values minus pooled slope times average of X values.

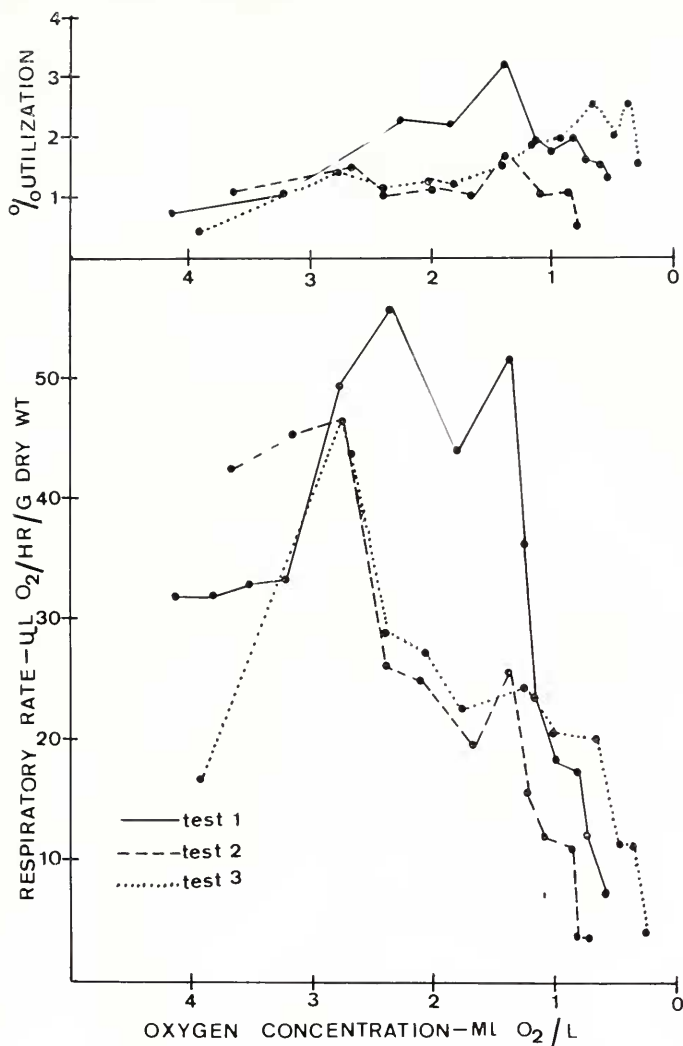


FIGURE 1. Rate of oxygen uptake ($\mu\text{l O}_2/\text{hr/g}$ dry weight) and percent utilization of available oxygen by *Mellita quinquesperforata* in decreasing oxygen concentrations in three representative experiments. A closed system was used for measurement.

RESULTS

Rates of respiration of *Mellita quinquesperforata* conform to oxygen concentrations in water (Fig. 1). Oxygen consumption decreases with decreasing oxygen pressure in a nearly linear manner. At very low levels of external oxygen (< 1 ml O_2/liter), a low level of respiration is maintained.

In monthly oxygen measurements at ambient temperatures, rates of respiration are dependent on both body weight (wet, dry or body nitrogen) and water

TABLE I

Summary of linear regression equations for ml O₂ respired/hr per animal vs. dry body weight in non-starved *Mellita quinqueperforata* at monthly ambient water temperatures and in starved sand dollars for various periods of starvation at ambient water temperatures. The form of the linear regression equations is log₁₀ ml O₂ respired/hr per animal (Y) equals log₁₀ g dry body weight (X) times slope plus intercept. A closed system was used for measurement.

Date	Dry weight of animals (g)	Ambient water temperature (°C)	# days starved	N	Slope	"r" for slope	Intercept	Intercept (adjusted)
Non-starved animals								
VII/4/72	1.5-26.5	31	—	5	0.5448	180.81**	-0.7508	-0.7541
VII/25/72	0.3-17.6	30	—	6	0.5754	61.46**	-0.9960	-0.9707
VIII/30/72	2.2-16.0	33	—	6	0.5799	41.44**	-0.8954	-0.8655
IX/30/72	1.0-21.9	27	—	5	0.5174	49.88**	-0.9671	-0.9908
X/24/72	0.4-26.8	25	—	5	0.6221	308.72***	-1.0426	-1.0027
XI/15/72	1.0-15.4	22	—	5	0.5136	1167.25***	-0.9850	-1.0119
XII/15/72	2.4-15.9	20	—	6	0.5285	18.55**	-1.0351	-1.0717
I/16/73	2.0-13.8	20	—	6	0.5116	30.17**	-0.9377	-0.9876
II/27/73	4.1-12.0	15	—	6	0.6093	10.59*	-1.1714	-1.1174
V/14/73	1.7-35.8	28	—	6	0.6704	21.60**	-1.0208	-0.8706
Starved animals								
VI/30/72	0.6-54.6	30	5	5	0.8410	56.02***	-1.1018	
VII/21/72	3.1-23.4	31	18	4	0.7011	14.75**	-1.2526	
X/16/72	0.5-29.0	25	20	5	0.9297	106.48**	-1.3979	
VIII/14/73	2.4-14.2	29	24	5	0.9600	17.29*	-1.3739	
XI/15/73	2.0-28.2	21.5	12	5	0.2978	1.32	-0.8849	

* Significant at 95% level.

** Significant at 99% level.

TABLE II

Summary of analysis of covariance for testing significance of differences between slopes and intercepts for regression equations of oxygen uptake in *Mellita quinqueperforata* at different temperatures, in different nutritional states, on a dry (DW) and nitrogen (NW) weight basis, and in closed and open respirometers. The form of the linear regression equation is \log_{10} ml O₂ respired/hr per animal (Y) equals \log_{10} g dry body weight or nitrogen weight (X) times slope plus intercept. For comparing slopes, summer months are considered as VI, VII, and VIII; fall months are IX, X, and XI; winter months are XII, I, and II; and spring months are III, IV, and V.

Dates or experiments being tested	Pooled slope	χ^2 variance	"F" for slope	df	"F" for intercept	df
Tests for heterogeneity among experimental dates						
All non-starved dates (DW)	0.5485	13.61	0.3027	9, 36		
Summer non-starved dates (DW)	0.5374	5.10	0.1323	2, 11	21.7575**	2, 27
Fall non-starved dates (DW)	0.5614	4.20	2.2056	2, 9	0.3768	2, 23
Winter non-starved dates (DW)	0.5327	0.90	0.0827	2, 12	7.8714**	2, 29
All non-starved dates (NW)	0.5670	14.55	1.1036	8, 32	1154.6722**	8, 327
All starved dates (DW)	0.8216	2.37	1.5747	4, 14		
All starved dates (NW)	0.8132	7.77	2.5699	4, 14	15.9071**	4, 75
Tests for heterogeneity among grouped regressions						
Starved vs non-starved summer dates (DW)	0.5789	0.83	7.7766**	1, 24	2.3639	1, 25
Starved vs non-starved fall dates (DW)	0.6611	15.43**	6.2446**	1, 21	1.8405	1, 27
Starved vs non-starved summer dates (NW)	0.6359	0.01	2.1658	1, 21	0.0364	1, 22
Starved vs non-starved fall dates (NW)	0.6572	10.42**	2.9027	1, 21	0.2687	1, 22
Closed vs open at 25° C	0.6772	1.09	0.0750	1, 8	62.4133**	1, 9
Closed vs open at 20° C	0.5496	0.90	0.0436	1, 26	23.2153**	1, 27
Closed vs open at 30° C	0.4115	12.52**	0.0456	1, 20	11.8181**	1, 21

* Significant at 95% level.

** Significant at 99% level.

temperature (Table I; Fig. 2). Small animals have proportionally higher rates of respiration than do large animals when values are expressed on a dry weight (pooled yearly slope of 0.5485; Table II) or a nitrogen weight (pooled yearly slope of 0.5670; Table II) basis. Differences between slopes are not significant when slopes are compared together by year or by season (Table II). Degree of gonadal development had no effect on respiratory rates.

Although there was no significant difference between slopes, rates of respiration did change significantly with water temperature, as indicated by significant "F" values for intercepts (Table II). To simplify comparison at different temperatures, intercepts were adjusted using a pooled slope of 0.5485 (monthly slopes were not significantly different) for all experiments. Using these adjusted intercepts, a 5-g animal (dry weight) would have highest rates of respiration on VII/4/72 at 31° C (0.4259 ml O₂/hr) and lowest rates on II/27/73 at 15° C (0.1845 ml O₂/hr) (Fig. 2). Rates of respiration slowly decrease between 30 and 22° C (fall months) but decline greatly between 31 and 30° C (VII/4/72 and VII/25/72, respectively). The respiratory rate is lower at 33° C than at 31° C (Fig. 2). Q₁₀ values for field acclimatized animals are 1.38 from the temperature range 15 to 33° C, 1.69 from 15 to 31° C, 1.93 from 22 to 31° C, 1.13 from 22 to 30° C and 1.42 from 15 to 22° C.

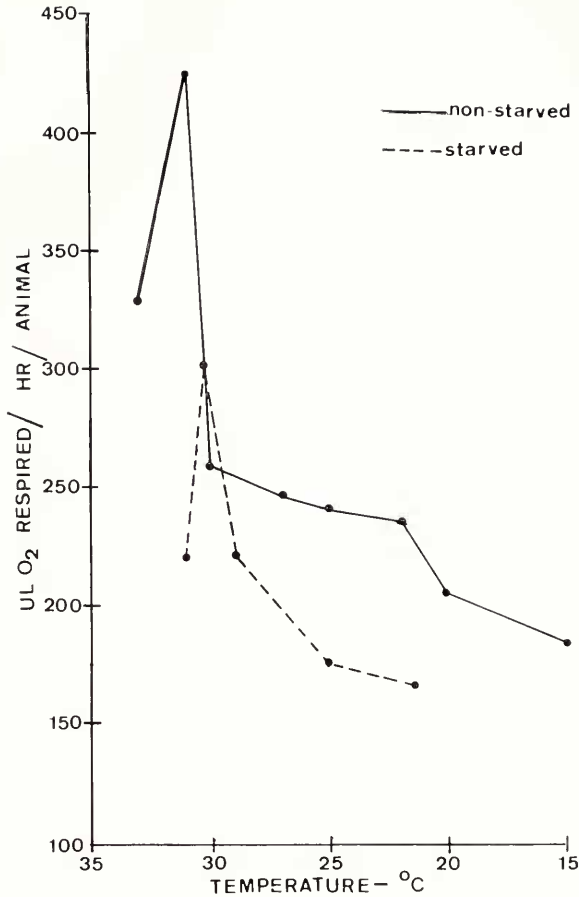


FIGURE 2. Relationship between oxygen consumption ($\mu\text{l O}_2$ respired/hr per animal) and water temperature for a starved and a non-starved 5-g (dry) specimen of *Mellita quinquiesperforata*. Rates were calculated from regression equations given in Table I.

Respiratory rates decline with starvation; the degree to which the rate declined depended on length of time animals were starved, water temperatures during starvation, and weight of the animal. Because animals were starved for different lengths of time at different water temperatures, it is difficult to assess the effect of these variables independently. Respiratory rates became more depressed as the period of starvation increased (Table I). A 1-g dry animal which was starved for 18 days at 31° C (VII/21/72) would use 53.63 $\mu\text{l O}_2$ /hr, whereas a 1-g animal starved for 5 days at 30° C (VII/30/72) would use 76.24 $\mu\text{l O}_2$ /hr (calculated using a pooled slope of 0.8670 and adjusted intercepts, Table I).

Effects of starvation depend on weight of the animals. On the basis of body dry weight, starvation has a proportionally greater effect on the respiratory rate of small starved animals as indicated by higher values for "starved" slopes (Table I). A 20-g (dry weight) starved animal has slightly higher rates and a

5-g (dry weight) starved animal has lower rates when compared with non-starved animals of similar size (Table I; Fig. 2). On a seasonal basis, the slopes for starved and non-starved animals are significantly different (Table II).

When respiratory rates are expressed on a nitrogen basis, O_2 uptake of small, starved animals is not as depressed when compared to non-starved animals (Fig. 3) and the regression slopes and intercepts of the two groups are not significantly different (Table II). Starved animals of all sizes have significantly less nitrogen/g dry weight than non-starved animals (Lane, 1977; Fig. 4) and small animals lose (metabolize) slightly more nitrogen during starvation than do larger animals (Lane, 1977). Small animals have lower rates of respiration when starved, but they have less body nitrogen as well when compared with larger animals.

Rates of respiration depend on the type of system used for measuring respiration. Comparison of respiration in closed and open systems at the same temperature shows intercepts, hence rates, of O_2 consumption are significantly higher in the open system (Table II). Using pooled slopes and adjusted intercepts for each

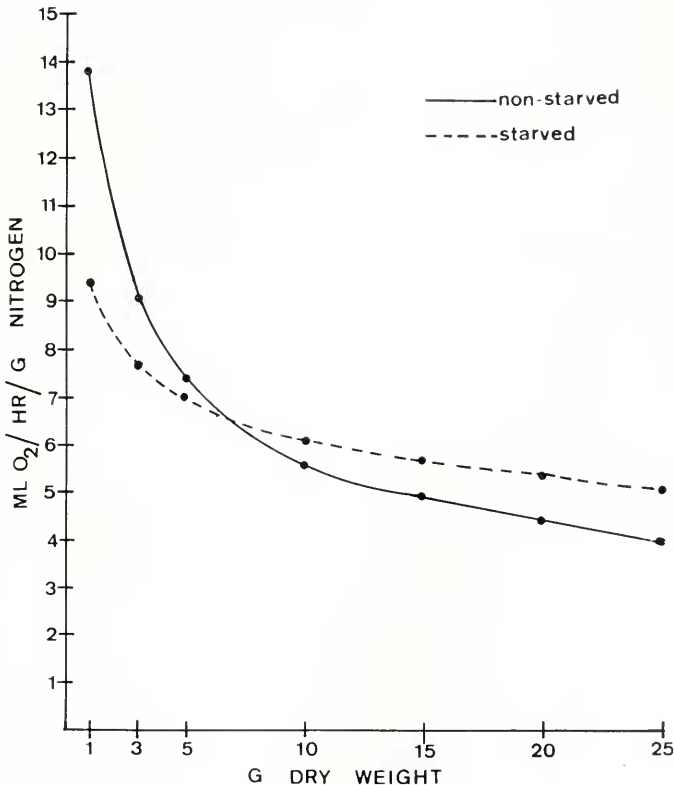


FIGURE 3. Relationship between oxygen consumption (ml O_2 respired/hr/g nitrogen) and dry body weight for starved and non-starved specimens of *Mellita quinqueperforata* at fall water temperatures. Rates were calculated as follows; non-starved animals- \log_{10} ml O_2 /hr/g nitrogen equals 1.1414 minus 0.3823 times \log_{10} g dry body weight; starved animals- \log_{10} ml O_2 /hr/g nitrogen equals 0.9740 minus 0.1835 times \log_{10} g dry body weight.

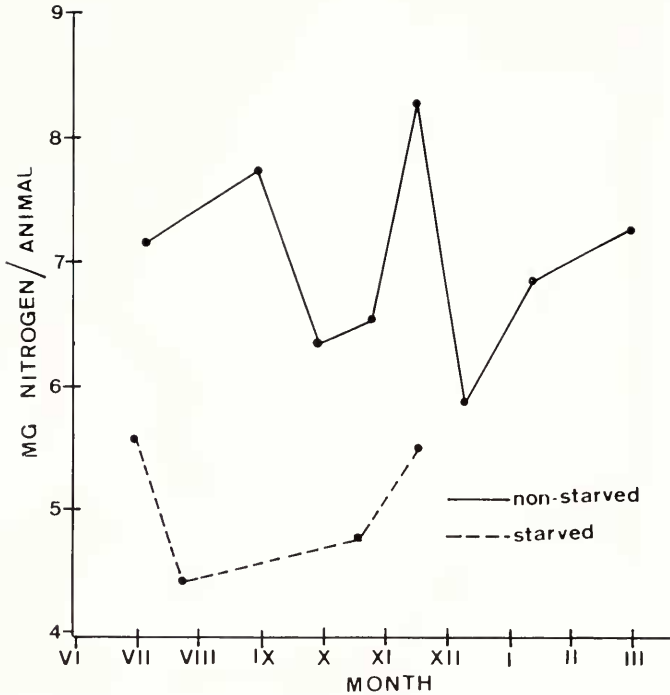


FIGURE 4. Seasonal changes in the amounts of total nitrogen in a starved and non-starved 1-g specimen of *Mellita quinquesperforata*. Values were calculated using pooled seasonal slopes and adjusted intercepts. Slopes used for non-starved animals are: summer, 0.8989; fall, 0.9462; winter, 1.0301. Slopes used for starved animals are: summer, 0.9561; fall, 1.0499.

temperature, a 10-g animal (dry weight) would respire 0.3003 ml O₂/hr per animal and 1.0598 ml O₂/hr per animal at 25° C; 0.2252 ml O₂/hr per animal and 0.5564 ml O₂/hr per animal at 20° C; and 0.4990 and 0.8158 ml O₂/hr per animal at 30° C in closed and open systems respectively. Comparison of respiration during the day and night in an open system showed no trends.

DISCUSSION

As found with many other echinoderms and invertebrates in general, the respiratory rates of *Mellita quinquesperforata* are modified by a variety of factors. Body weight or age is one such factor. Smaller (younger) animals have proportionally higher rates of respiration than larger (older) animals when rates are based on both body weight or body nitrogen. Similarly, this effect of size (age) on rate of O₂ uptake has been found in all other echinoids studied and regression slopes (log₁₀ ml O₂ respired/hr per animal versus log₁₀ body weight) for echinoids generally fall between 0.500 and 0.700 (Lewis, 1967, 1968; McPherson, 1968; Percy, 1971; Webster, 1972; Miller and Mann, 1973). An adequate or complete explanation for this phenomenon is lacking. The decreasing surface area with increasing weight explanation does not appear to apply in the case of *M. quinques-*

perforata. Surface area (from shape) is approximately body weight 0.66, while respiration is body weight 0.5485. In addition, the body wall of echinoids has been shown to be the principal consumer (90%) of oxygen in whole respiring animals (Giese, Farmanfarmaian, Hilden, and Doezema, 1966; Webster, 1972; Belman and Giese, 1974; Webster and Giese, 1975). Stephans, Volk, Wright, and Backlund (1978) similarly concluded that the epidermis of the test of the sand dollar, *Dendraster excentricus*. Since the outer surface of the body wall is directly exposed to oxygenated water, the surface to volume argument should hardly apply to these echinoids.

In *M. quinquesperforata*, it would appear that smaller (younger) animals may simply have 'faster' metabolic systems, i.e., shorter half-lives of enzymes, faster turnover of proteins. Evidence for this comes from similar decreases in rate with increasing animal weight which were found for the processes of feeding, carbon excretion, ammonia excretion and radioactive uptake in this sand dollar (Lane, 1977). With starvation, smaller sand dollars metabolize proportionally greater amounts of nitrogen than larger animals. Fuji (1962, 1967) and Miller and Mann (1973) found similar allometry in different functions of other echinoids. Stephans *et al.* (1978), however, found that differences in rates of amino acid uptake between small and large sand dollars disappeared when surface area was used as the basis of expression.

As with *M. quinquesperforata*, other echinoids have depressed respiratory rates with starvation. Farmanfarmaian (1966) observed that V_{O_2} 's were reduced by as much as 50% after a month of starvation. Giese (1967) noted a general

TABLE III

Summer and fall comparisons for calories expended in respiration month of starved and non-starved Mellita quinquesperforata. For starved animals, values were calculated from VIII 14 72 (summer) with a slope of 0.867 and an adjusted intercept of -1.3353 and XI 15 73 (fall) with a slope of 0.7720 and an adjusted intercept of -1.3099. For non-starved animals, a slope of 0.5485 and an adjusted intercept of -0.7541 (VII 4 72) was used for calculating summer values and a slope of 0.5485 and an adjusted intercept of -1.0119 (XI 15 72) was used for fall values. 4.8 cal/ml O₂ respired was used to convert ml O₂ into calories.

Dry weight of animals	Cal respired/ month/starved animal	Cal respired/ month/non-starved animal	Starved values/ non-starved values × 100
Summer comparison			
1 g	159.67	608.80	26.22%
10 g	1175.71	2152.65	54.61%
20 g	2144.11	3148.39	68.10%
40 g	3910.80	4604.72	83.93%
Fall comparison			
1 g	169.31	336.26	50.35%
10 g	1001.55	1188.98	84.23%
20 g	1710.05	1738.95	98.33%
40 g	2919.97	2543.33	114.80%

decline in rate of oxygen uptake over a month of starvation. Webster (1972) found that the greatest decrease in V_{O_2} occurred in the first week of starvation with little change thereafter. Boolootian and Cantor (1965) reported that the respiratory rate fell to a low level after three weeks of starvation and remained constant thereafter. Differences in response of respiratory rate among echinoids with starvation may perhaps be explained by differences in nutritional history at the beginning of the experiment and consequent differences in substrate being metabolized during starvation. Wallace (1973) found that the V_{O_2} of starving crabs fell in steps corresponding to the type of nutrient reserve being metabolized. Carbohydrate reserves were first utilized, with lipid next and protein last. Differences in response of small and large specimens of *M. quinquesperforata* to starvation may also be due to differences in substrate being metabolized. If so, large animals may have had proportionally greater reserves of either carbohydrate or lipid (in the gonad). Consequently, small animals may have been metabolizing protein while larger animals were metabolizing carbohydrate or lipid, resulting in more depressed rates of respiration in small animals. The proportionally greater decrease in amount of body nitrogen in small, starved animals seems to support this conclusion.

Higher rates of respiration in small, non-starved specimens of *Mellita* may also have been due to effects of SDA or greater activity in non-starved sand dollars. Effects of both factors, however, appear to be minimal. Activity of starved and non-starved animals was similar in closed containers. As reported by Lilly (1979) for two species of sea urchins, the effect of SDA was most pronounced just after feeding and declined to pre-feeding levels after 3 hr. Rates of O_2 uptake in the sand dollar were measured approximately 24 hr after feeding. Hence SDA should be of slight consequence.

Differences between respiratory rates in starved and non-starved animals may represent energy used in growing (Table III). If so, 26% of respiration energy is used for summer maintenance and the remainder (74%) is energy expended for growth in a 1-g, non-starved specimen of *M. quinquesperforata*. In an actively growing 20-g animal (dry weight), 68% of the respiration energy is used for summer maintenance and 32% represents energy for growth (Table III). In fall, more non-starved respiration energy is used in maintenance and less in growth for all size sand dollars. Both the greater amounts of energy expended in growth by small sand dollars and the seasonal difference in amounts of energy for growth by all size animals are consistent with information from growth studies on this animal (Lane, 1977). From growth studies, a 1-g animal would expend 136 calories for growth/month in the summer (Lane, 1977). Difference between respiratory rates of starved and non-starved 1-g animals indicate 449 calories/month would be spent in growth. Likewise in fall, a 1-g animal would add 91 calories/month in growth (Lane, 1977) and expend 167 calories/month in growing (from difference between starved and non-starved respiration). For larger animals in fall, starved respiration was greater than non-starved. This anomaly may have resulted from differences in the nutritional condition of "freshly collected" animals. Negative growth reported for large animals in fall (Lane, 1977) could indicate that "freshly collected" specimens of *M. quinquesperforata* were

already starved when taken from the field, and starvation in the laboratory produced no further change in respiratory rate.

Although laboratory experiments were not specifically designed to characterize type of acclimation response in *M. quinquesperforata*, monthly oxygen measurements made at ambient water temperatures did demonstrate partial acclimatization in sand dollars. V_{O_2} 's were higher in January at 20° C than in December at the same temperature. Likewise, acclimatization to summer water conditions may have resulted in lower rates of respiration on VII/25/72 at 30° C as compared to the much higher rates three weeks earlier on VII/4/72 at 31° C. As with many other echinoids (Farmanfarmaian and Giese, 1963; Moore and McPherson, 1965; McPherson, 1968; Percy, 1971; Webster, 1972), this compensatory response was only partial in *Mellita* since respiration was still higher in summer than in winter.

The sensitivity of the respiratory rate in *M. quinquesperforata* (Q_{10}) was relatively low between 22 and 30° C. In the Tampa Bay area, the change in water temperature over the 22 to 30° C range is rapid during the spring warming and fall cooling. The respiratory insensitivity over this range would, therefore, appear to have some adaptive value. The decline in V_{O_2} at 33° C may indicate metabolic malfunction as this temperature is close to the lethal limits ($\sim 38^\circ$ C) of this sand dollar.

Oxygen consumption may be modified by type of system used for measuring respiration. Miller and Mamm (1973) for *S. droebachiensis*, Webster and Giese (1975) for *Strongylocentrotus purpuratus* and this study found that rates of respiration were higher in flow-through systems when compared with closed systems. Although this increased rate may be caused by increased availability of oxygen, activity of animals may also be increased in flowing water. Activity of *M. quinquesperforata* was much greater in the flow-through system than intermittent activity of sand dollars in closed systems. Although sand dollars are exposed to a continual exchange of water in their environment, much of the time they are partially buried and do not or can not continually wave their spines back and forth as was the case in the open system. Therefore, the monthly oxygen measurements made in closed dishes are considered more representative of routine metabolism.

Due to various factors which modify metabolic rate, and the different units used to express respiratory rate, it is difficult to compare absolute rates of respiration among various echinoids. When compared to the respiratory rates of tropical and temperate echinoids as given by Webster (1975), V_{O_2} 's of *M. quinquesperforata* (as found in this study) are slightly higher than rates for tropical echinoids of similar weight.

SUMMARY

1. Rates of respiration in a closed vessel conformed to oxygen concentrations in surrounding water until a low level (1 ml O_2 /liter) of oxygen was attained.
2. Respiratory rates of small animals were proportionally higher on both a dry weight and nitrogen weight basis than rates of large animals (slope for ml O_2 respired/hr per animal was 0.5485 for dry weight and 0.5670 for nitrogen) in a closed vessel.

3. Respiratory rates of field acclimatized animals were slightly higher at summer temperatures (30–33° C) than at winter water temperatures (15–20° C) with evidence for partial acclimatization presented.
4. Respiratory rates of starved animals were lower than rates of non-starved animals with starvation depressing the rates of smaller animals more than rates of larger animals.
5. Respiratory rates in an open system were approximately twice as high as rates in a closed system due to greater activity of animals in the open system.
6. Comparison of day versus night respiration showed no obvious trends.
7. Respiratory rates of *M. quinqueperforata* are slightly higher than rates of a similar weight, tropical, regular urchin as reported in the literature.

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